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SPATIAL AND TEMPORAL PATTERN IN LENGTH-MASS REGRESSIONS OF FRESHWATER GASTROPODS IN NEVADA SPRING ECOSYSTEMS

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ABSTRACT

We developed length-mass regressions for 16 aquatic gastropods collected from 27 springs
in Nevada, United States. The relationship between shell length and body mass for all spe-cies was best described by fitting a power function. The mean value of the exponent b (2.40 + 0.39) was lower than reported for other aquatic gastropods, particularly for smaller genera, such as Pyrgulopsis and Tryonia. Length-mass regressions of gastropods showed intraspe-cific variation, as well as spatiotemporal variation among the same species. Certain habitat characteristics, especially water temperature, may play a key role in determining growth rates and ultimately length-mass regressions in this study. Although the power term b showed high variability when the same species (Melanoides tuberculata, Pyrgulopsis lockensis, and Pyrgulopsis turbatrix) were collected from different springs, the power term was similar when the same species (Pyrgulopsis marcida) was collected from the same spring during different seasons and years. Therefore, we suggest that published equations should be used with caution and only when habitat characteristics and length ranges are similar compared to those in the literature.
Key words: gastropods, length-mass regressions, power term, spring ecosystems, Nevada.

INTRODUCTION

Aquatic gastropods are ubiquitous and inhabit
many spring-related water bodies scattered
throughout the southwestern United States
(Hershler, 1994; Hershler & Sada, 2002; Un-
mack & Minckley, 2008). It has been recognized that the disconnection of springs from other water bodies after the Pleistocene era and their long-term isolation have led to habitat fragmentation and, in turn, to distinct gastropod population distributions, population genetics and speciation (Hershler, 1994). Particularly for species belonging to Pyrgulopsis (Hydro-biidae), local endemism is common, and many species are restricted to a single spring, spring complex or drainage system (Hershler, 1984, 1998). Their presence indicates the long-term, stable conditions of certain habitat character-istics and that many gastropods have evolved in isolation over time (Frest & Johannes, 1995; Sada & Vineyard, 2002).
Assessing the importance of those aquatic gastropods in energy and nutrient transfer between trophic levels, as well as nutrient recy-

cling, requires information about their biomass (Benke et al., 1999; Hall et al., 2003; Silva et al., 2010). However, determining biomass, particu-larly of small gastropods (e.g. Pyrgulopsis and Tryonia) by direct measurement is often difficult and time consuming. Furthermore, in many cases the direct measurement of dry mass is often hindered by an incomplete specimen, ei-ther because soft tissue is partly digested from chemical preservation or from passing through the digestive systems of predators so that only the shell is left behind (Hödar, 1997). Awidely accepted tool for estimating biomass, growth rates and/or secondary production of benthic invertebrates in ecological studies is length-mass regression (Benke et al., 1999; Gruner, 2003; Becker et al., 2009). By using the power function DM = aLb, dry mass can be derived as a power oft he linear dimension of an organism, where DM is the dry mass (in mg),
L is the body length (for this study, shell length
in mm), and a and 6 are constants (Benke et
al., 1999). The power function can also be
expressed in a linearized form as: log:, DM =
log408 + (b x logy) L). The term b describes how

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FIG. 1. Map of Nevada indicating the sampling locations.

body proportions change with increasing size
during ontogeny (Hirst, 2012). A value close to 3
indicates isometric enlargement (i.e., the body
proportions remain constant during growth),
whereas a value less than 3 implies a relative
increase in elongation (Hirst, 2012). Information about changes in body shape during ontogeny is essential for predicting further biological and ecological consequences. For example, Glazier (2010) showed that metabolic-rate scaling is related to changes in body shape during on-togeny and that even closely related species can exhibit significant variation in respiration scaling.
The advantage of estimating dry mass (DM) using length-mass regressions is that they not only provide rapid measurements, but also allow the biomass of already extinct spring gastropod populations to be reconstructed using preserved shells. Although length-mass regressions have been applied to many terres-trial and aquatic invertebrates, there are only few studies that have analyzed length-mass relationships for spring-dwelling gastropods (e.g., Elkarmi & Ismail, 2007). The long-term adaption of most of the spring-dwelling gas-tropods makes them the ideal subjects for studying the link between long-term, stable conditions and length-mass relationships in crenic food webs. Moreover, when springs are

persistent, they are generally more stable than lotic and lentic systems because they are not exposed to seasonal variability in water chem-istry, temperature, and discharge (McCabe, 1998). These characteristics suggest that the processes that determine growth rates and consequently the intraspecific length-to-mass scaling of spring-dwelling gastropods during ontogeny might be trenchantly different from gastropods that inhabit lentic and lotic eco-systems. The overall objective of this study was to develop length-mass regressions from spring-dwelling gastropods to predict DM from the shell lengths of the major gastropod spe-cies in spring ecosystems along a temperature gradient in Nevada. The occurrence of the same species in multiple springs during differ-ent seasons allowed us to test the spatial and temporal effects on length-mass relationships (i.e., variations in the b value).

MATERIALS AND METHODS

Study Sites

Twenty-seven springs were selected accord-ing to the historical and recent occurrences of spring-dwelling gastropods (Fig. 1). The springs are situated in the Great Basin Prov-

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ince in southern and central Nevada and range from 469 m to 2,002 min elevation. The springs are widely separated by vast areas with little or no evidence of groundwater discharge. The springs themselves have nearly constant dis-charge and probably represent points or zones of principal discharge from large regional flow systems. The Cenozoic sand and gravel de-posits of the overlying basin-fill aquifer readily yield water to springs and wells, which are the major water supply for agricultural, livestock, and municipal use (Harrill & Prudic, 1998; Welch et al., 2008). Groundwater quality in this region is characterized by low dissolved oxygen and low nitrate concentration (2.5 mg/L and < 1 mg/L, respectively) and a high total dissolved solids concentration (410 mg/ L on average) (Berndt et al., 2005). Springs fed by local aquifers usually have cooler tempera-tures because the water stays in the ground for shorter periods of time. The temperature in the study region ranges from -11°C to -2°C in the winter and 18°C to 27°C in the summer, which is typical of the Great Basin Desert. Annual precipitation varies greatly between valley locations, ranging from 20 cm to 38 cm annually (Hershey et al., 2007).

Biological Sampling

A total of 1,451 gastropods belonging to three families (Hydrobiidae, Physidae, and Thiaridae) and 16 species were collected in April 2010, May 2012, and June 2012 by either washing substrates (rocks, wood, macrophytes) or sifting fine sediments with a 250 um sieve. Gastropods were put in filtered spring water for one hour to ensure that they emptied their guts. Water temperature was recorded at each site during collection using an YSI-model 650 MDS temperature-oxygen meter. A one-liter water sample was collected from each spring for nitrate-nitrogen (NO3-N), soluble reactive phosphorus (SRP), and chlo-rophyll a (СШ a) analysis.
Gastropods from each spring were identified by gastropod expert Donald W. Sada of the Desert Research Institute in Reno, Nevada, based on shell characteristics and penial mor-phology (for details see Hershler, 1998) and by using collections of preserved gastropod of all the populations in their original description sampled in this study (Sada, 2008; Hershler & Sada, 1987, 2001, 2002). The species identification has also been verified by Rob-

ert Hershler of the Smithsonian Institution in Washington, D.C.
In the laboratory, undamaged gastropods were dried at 50°C for 72 h until the weight was constant. To obtain DM, gastropods were weighed individually to the nearest 0.01 mg on a Mettler Toledo New Classic MS balance. Body length (BL) was expressed as the maxi-mum shell length (the distance between the tip of the apex and the edge of the bottom lip) and was measured with calipers to the nearest 0.01 mm. Water samples from each spring were analyzed for NO3-N and SRP at the Desert Research Institute’s Water Analysis Laboratory (Reno, Nevada) using standard EPA methods (U.S. Environmental Protection Agency, 1979). We determined Chl a for each spring spectro-photometrically by measuring the absorbance of algae pigments from a known volume of water. The Chl a concentration (ug/L) was used to represent the primary producer’s biomass (i.e., food availability).

Statistics

The power function M = aLb was applied exclusively to all taxa because this function yielded the highest coefficient of determination (r2). Analysis of covariance (ANCOVA) was used to test for differences in the slope of the length-mass regression equations among all gastropod species. We used the most abun-dant species found at multiple springs during different years and seasons — Melanoides tu-berculata (Muller, 1774), Pyrgulopsis lockensis Hershler, 1998, Pyrgulopsis turbatrix Herschler, 1998, Pyrgulopsis marcida Herschler, 1998, and Physa acuta (Draparnaud, 1805); see Table 1 for the spring names where each spe-cies was collected — to test for differences in the length-mass regressions. The ANCOVA was used when (i) the same species were sampled from different springs (Melanoides tuberculata, Pyrgulopsis lockensis, Pyrgulopsis turbatrix, and Physa acuta) and (ii) the same gastropod species were sampled from the same spring during different years and seasons (Pyrgulopsis marcida). In this case, the “site” was the categorical variable, "body length” was the regressor variable (x), and body mass was the response variable. Univariate linear regres-sions were used to test for any correlations be-tween physicochemical variables. All statistical analyses were done in SAS (version 8.2; SAS Institute, Cary, North Carolina).

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FIG. 2. Comparison of composite length-mass regressions for four gastro-pod genera (Pyrgulopsis, Tryonia, Melanoides, and Physa) based on shell length (mm) and dry mass (mg, including shell).

RESULTS

The 27 springs exhibited a wide range of physicochemical characteristics. The water temperature ranged from 10.9°C to 36°C and NO:-N and SRP ranged from 0.004 mg/L to 1.77 mg/L and 0.002 mg/L to 0.49 mg/L, respectively (Table 1). Although there was a significant negative correlation between tem-perature and МО.-М (r2 = 0.32, р = 0.0008), there was no correlation between temperature and SRP (r2 = 0.04, p = 0.266) or SRP and МО.-М (r2 = 0.08, р = 0.119). However, there was a significant positive correlation between temperature and Chl a (r2 = 0.57, p < 0.001). Body length (p < 0.001) significantly predicted DM for all taxa, which was shown by high co-efficients of determination (range: 0.65-0.99) (Table 1). On average, the power term b was 2.45 + 0.39 when all gastropods were pooled together. There was a significant difference in the length-mass regressions between the four gastropod genera (ANCOVA, p < 0.001, Fig. 2). Thiaridae (Melanoides tuberculata) had the highest mean b values (2.82 + 0.15), whereas Tryonia (Tryonia spp.) had the lowest mean b values (1.99 + 0.64). The shell lengths of the Tryonia genera collected from two springs were significantly different (ANOVA, p < 0.001). This caused a much higher mean b value in Figure 1 (b = 2.69) when individuals from the two springs were pooled in the length-mass regression. The mean b values of Pyrgulopsis and Physa were 2.04 + 0.37 and 2.58 + 0.22, respectively. The length-mass regressions for four genera (M. tuberculata, P. lockensis, P.

turbatrix, and Р acuta) collected from dif-ferent springs during different seasons are presented in Figure 3. The power term b was similar (range: 2.50-2.68) among P. lockensis collected in summer from springs that are located close together, but not for the Р lockensis sampled from Hay Corral Spring, which had a much lower power term b (b = 1.74, Fig. 3a). There was a significant effect of BL x site interaction (р < 0.001), indicating that the slopes of length-mass regressions of P. lockensis were different between the four sites. We also found a significant effect of BL (p < 0.001) and an effect of site (p < 0.001), which were most likely due to the very small power term of 1.74 for individuals collected from Hay Corral Spring. There was a significant effect of BL (p < 0.001) and site (p < 0.001) on the slope of the length-mass regression of M. tuberculata (p < 0.001, Fig. 3b). However, there was no effect of site x BL interaction (p = 0.4043), indicating that the slopes of the length-mass regressions were not significantly different among the four sites. The b values of P acuta sampled in different springs showed some variation, but the effect of site x BL interaction was only marginally significant (р = 0.055), indicating that the slope of regressions between the three springs are only slightly different (Fig. 3c). There was a significant effect of BL (p < 0.001), but no effect of site (p = 0.349). A large range in the power term b, from 2.15-2.91, was found for the Р turbatrix collected from four springs that are located far apart (Fig. 3d). There was a significant

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FIG. 3. Length-mass relationships for Pyrgulopsis lockensis. A: Power term b values for ReynolAd 2s.6 1, Reynolds В 2.68, North Lockes 2.50, and Hay Corral 1.71, Melanoides tuberculata; В: Power term b values for Moorman 3.01, Blue Point 2.78, Rogers 2.83, and LWS 2.65, Physa acuta; C: Power term b values for Lost Creek 2.67, CR12-53 2.24, and Bennett 2.40, and Pyrgulopsis turbatrix; D: Power term b values for Grapevine 2.35, Horseshoe 2.41, La Madre 2.91, and Willow Source 2.51).

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FIG. 4. Length-mass relationships for Pyrgulopsis
marcida collected from Hardy Springs in two dif-ferent seasons and years (power term b values for spring 2011: 2.15, and summer 2012: 2.18).

effect of BL (p < 0.001), an effect of site (p < 0.001), and a significant site x BL interaction (p = 0.0037), indicating that the slopes of the length-mass regressions of P. turbatrix were different between the four sites.
Individuals belonging to P. marcida were col-lected from the same spring (Hardy Springs) during different seasons and years (April 2011 and June 2012). The power terms b were 2.14 and 2.17, respectively, even though individuals sampled in summer 2012 had a significantly larger BL compared to individuals sampled in spring 2011 (t-test, p < 0.001; Fig. 4). Site had a marginally significant effect (p = 0.0457). However, BL х site interaction had no effect on the slope of the length-mass regression of P. marcida (р = 0.1997), indicating that the slopes of length-mass regressions were similar between seasons.

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DISCUSSION

Body length was a good predictor of DM of
aquatic gastropods. In accordance with other
studies, the relationship between gastropods’
linear body dimension and dry mass was best explained using a power function over the ex-ponential model (e.g., Rosemond et al., 1993; Benke et al., 1999; McKinney et al., 2004). The mean of the power term b was lower than 3 (2.44 + 0.37) for all genera combined, indicating an elongation in shape during ontogeny in our gastropods (Hirst, 2012). Our data suggest that long-term adaption of gastropods to a certain spring ecosystem might affect length-mass relationships. First, when the same species was sampled from different springs, they showed significant variation in the power term b. Sec-ond, when the same species was sampled from the same spring during different years and seasons, they only showed slight variations in the power term b. Several explanations-which are not necessarily exclusive-that may explain these patterns in length-mass regressions are proposed here.
Most of the Pyrgulopsis and Tryonia genera are tightly linked to running water close to spring sources (Hershler, 1998). Therefore, Pyrgulopsis might increase their body length more rapidly than their body diameter during ontogeny and become proportionately narrower to withstand the higher flow velocities around the spring head. In contrast, b values of M. tuberculata were around 3. This exotic mollusk prefers slow-flowing or standing water bodies (de Kock, 2009), which is probably one reason for the isometric enlargement. Unfortunately, we did not measure flow velocities in our study springs. Therefore, this assumption needs to be tested further by recording flow velocities and/or shear stress at sites where gastropods are being collected.
Temperature is a key component that regu-lates fundamental biological processes, such as growth rates and body size (Angiletta et al., 2003; Woods et al., 2003). Previous studies on Pyrgulopsis bruneauensis showed an intimate relationship between temperature and growth rates (Mladenka & Minshall, 2001). Elkarmi & Ismail (2007) also reported differences in shell length between two M. tuberculata populations collected from hot springs and freshwater pools that differed in temperature. In our study, M. tuberculata were collected from springs ranging in water temperatures from 20.9°C to 36.2°C, which most likely caused differences

in growth and age. In contrast to Melanoides, the slopes for Physa sampled from multiple springs during different seasons did not vary significantly. Although those springs varied widely in NO3-N and Chl a, water temperature only varied by 0.4°C and 1°C, respectively. Therefore, it seems that water temperature is one of the most important variables affect-ing length-mass regressions of gastropods in this study. Water temperature has also been shown to affect gastropod shell plasticity and body mass, which consequently affects length-mass regressions. Trussel (2000) showed that phenotypic plasticity (i.e., the differences in shell morphology and body mass of Littorina obtusata) were in parts related to water tem-perature. We did not separate shells from soft tissue in our study. However, using an ash-free dry mass (dried material ashed at 550°C and reweighed) instead of the dry mass including the shell would have improved the detection of differences in shell morphology when cal-culating the soft-tissue-to-shell-mass ratio in same-sized individuals.
Contrary to the findings of Silva et al. (2010), growth rates of Melanoides in our study seem to be lower according to the power term b. This may be related to differences in food abundance and quality. The interaction of low food quantity and high population density has been shown to affect the shell length of Mytilus edulis (Alunno-Bruscia et al., 2001). To represent food quantity, we used the Chl a concentration, which was found to vary widely among our springs (3.3-55.9 ug/L) and was positively related to temperature. This is in-teresting because we expected a mutualistic effect of higher-temperature-related growth rates accompanied by higher food quantity. Fur-thermore, spring-dwelling gastropods such as Pyrgulopsis and Melanoides can reach densi-ties of > 1,000 individuals/m2 and > 1,500 indi-viduals/m2, respectively, in some of our springs (Hershler, 1998; Mehler, unpublished data). However, these high densities and the potential for greater food competition might have offset the favorable conditions of warm temperature and abundant food. Therefore, gastropods in those springs might increase in body length faster than they gain weight, ultimately causing b values to be < 3 due to the relative elongation in shape during ontogeny.
In contrast to the Pyrgulopsis species col-lected from different springs, the power term b of P marcida collected from Hardy Springs during different seasons and years was not

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significantly different. This indicates that growth rates between seasons and years are similar. When springs are persistent, they are generally more stable than lakes and streams because they are not exposed to seasonal variability in water chemistry, temperature, and discharge (McCabe, 1998; Cantonati et al., 2006). Therefore, we assume that growth rates of P. marcida are similar between seasons and years in long-term stable springs. We assume that growth variations within the same species are most likely caused by differences in the physical and chemical habitat characteristics. This is consistent with several other studies on benthic invertebrates and emphasizes the need to be cautious when using regressions for the same taxa from different regions (Meyer, 1989; Wenzel et al., 1990; Burgherr & Meyer, 1997). Moreover, an issue we want to address is the error that arises due to the potential misiden-tification of some of the gastropod species in this study. Gastropods belonging to the genera of Melanoides and Physa are very difficult to identify because of potentially different clonal lineages and a lack of shell characters, re-spectively (Samadi et al., 1999; Taylor, 2003). Therefore, it is possible that differences in growth rates and consequently the power term b might be the result of different clonal lineages and/or species.
Although there are several factors that affect the mass-length regressions of gastropods, we recommend considering water temperature in particular because of the tight interrelation of temperature, metabolic rates, and population growth (Savage et al., 2004). In accordance with other studies, collecting the full range of size cohorts can be as important to interpreting the power term b as sampling the same gas-tropod species in different geographic regions (Becker et al., 2009).
In conclusion, this study is one of the first to describe length-mass relationships for populations of gastropods from a wide range of spring ecosystems in Nevada. Our data can be used in further studies to determine growth rates, biomass, and the secondary production of aquatic gastropods. However, length-mass regressions obtained for gastropods in a spe-cific area are not generally transferable to other geographical regions, so particular emphasis should be given to the correct identification of species. Therefore, we recommend that the published length-mass regression should only be applied after a thorough review of habitat characteristics and observed length ranges.

To better understand variations of length-mass regressions even within the same species, fur-ther studies are necessary to determine which site-specific characteristics are most important in affecting growth and body size.

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LITERATURE CITED

ALUNNO-BRUSCIA, M., E. BOURGET & M. FRECHETTE, 2001, Shell allometry and length-mass-density relationship for Mytilus edulis in an experimental food-regulated situation. Marine Ecology Progress Series, 219: 177-188. ANGILLETTA, М. J., JR. 4 А. Е. DUNHAM, 2003, The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. The American Naturalist, 162: 332-342. BECKER, B., M. S. MORETTI & M. CALLISTO, 2009, Length-dry mass relationships for a typi-cal shredder in Brazilian stream (Trichoptera: Calamoceratidae). Aquatic Insects, 31: 227- 234.
ВЕМКЕ,А . C.,A . О. HURYN, L.A. SMOCK 4 J. В. WALLACE, 1999, Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society, 18: 308-343.
BERNDT, M. P., В. С. KATZ, В. D. LINDSEY, A. F. ARDIS & K. A. SKACH, 2005, Comparison of water chemistry in spring and well samples from selected carbonate aquifers in the United States. Pp. 74-81, in: E. L. Kuniansky, ed., U.S. Geological Survey Karst Interest Group Pro-ceedings, Rapid City, South Dakota, September 12-15, 2005. U.S. Geological Survey Scientific 1 Investigations Report, 2005: 5160. BURGHERR, P. 8 E. |. MEYER, 1997, Regres-sion analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. Archiv fúr Hydrobiologie, 139: 101-112.
CANTONATI, M., К. GERECKE 48 Е. BERTUZZI, 2006, Springs of the Alps-sensitive ecosystems to environmental change: from biodiversity as-sessments to long-term studies. Hydrobiologia, 562: 59-96.

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DE KOCK, K. N. & C. T. WOLMARANS, 2009, Distribution and habitats of Melanoides tuber-
culata (Müller, 1774) and M. victoriae (Dohrn,
1865) (Mollusca: Prosobranchia: Thiaridae) in
South Africa. Water SA, 35: 713-720.
DRAPARNAUD, J., 1805, Histoire naturele des molusques terrestres et fluviatiles de la France. Louis Colas, Paris, France, 614 pp.
ELKARMI, A. Z. & N. $. ISMAIL, 2007, Growth models and shell morphometrics of two popula-tions of Melanoides tuberculata (Thiaridae) liv-ing in hot springs and freshwater pools. Journal of Limnology, 66: 90-96. _
FREST, T. J. & E. J. JOHANNES, 1995, Interior Columbia Basin mollusk species of special concern. Final report: Interior Columbia Basin Ecosystem Management Project, No. 43-0E00- 4-9112. Walla Walla, Washington, 274 pp. GLAZIER, D. S., 2010, A unifying explanation for diverse metabolic scaling in animals and plants. Biological Reviews, 85: 111-138.
GRUNER, D. S., 2003, Regressions of length and width to predict arthropod biomass in the Hawai-ian Islands. Pacific Science, 57: 325-336. HALL, R. O., J. L. TANK & M. F. DYBDAHL, 2003, Exotic snails dominate carbon and nitrogen су-cling in a highly productive stream. Frontiers in Ecology and the Environment, 1: 408-411. HARRILL, J. R. & D. E. PRUDIC, 1998, Aquifer systems in the Great Basin region of Nevada, Utah, and adjacent States — a summary report. U. S. Geological Survey Professional Paper, 1409-13 A: 66 pp.
HERSHEY, R.L., V. M. HEILWEIL, P. GARDNER, В. Е. LYLES, $. EARMAN, J. М. THOMAS & К. W. LUNDMARK, 2007, Ground-water chemistry interpretations supporting the Basin and Range Regional Carbonate-rock Aquifer System (BAR-CAS) Study, eastern Nevada and western Utah. DHS Publication, 41230.
HERSHLER, R., 1984, The freshwater snails (Gastropoda: Rissoacea) of the Cuatro Cienga Basin: Systematic relationships and ecology of a unique fauna. Journal of the Arizona Nevada Academy of Science, 19: 61-76.
HERSHLER, R., 1994, A review of the North American freshwater snail genus Pyrgulopsis (Hydrobiidae). Smithsonian Contributions to Zoology, 554: 1-115. .
HERSHLER, R., 1998, A systematic review of the hydrobiid snail (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus Pyrgulopsis. The Veliger, 41: 1-132. HERSHLER, К. D. & W. SADA, 1987, Springsnails (Gastropoda:Hydrobiidae) of Ash Meadows, Amargosa basin, California and Nevada. Pro-ceedings of the Biological Society of Washing-ton, 100: 776-843.
HERSHLER, R. & D. W. SADA, 2001, Anew spe-cies of hydrobiid snail of the genus Pyrgulopsis from northwestern Nevada. The Veliger, 43: 367-375.
HERSHLER, К. & D.W. SADA, 2002, Biogeogra-phy of Great Basin freshwater snails of the ge-nus Pyrgulopsis. Pp. 255-276, in: R. HERSHLER, D. В. Mabsen & О. В. Currey, eds., Great Basin

aquatic systems history. Smithsonian Contribu-tions to Earth Sciences, 33: 405 pp.
HIRST, A. G., 2012, Intraspecific scaling of mass to length in pelagic animals: Ontogenetic shape change and its implications. Limnology and Oceanography, 57: 1579-1590.
HODAR, J. A., 1997, The use of regression equa-tions for estimation of prey length and biomass in diet studies of insectivore vertebrates. Mis-celania Zoologica, 202: 1-10.
McCABE, D. J., 1998, Biological communities in springbrooks. Pp. 221-228, in: L. BOTOSANEAU, ed., Studies in crenobiology. The biology of springs and springbrooks. Backhuys Publishers, Leiden, The Netherlands, 261pp.
McKINNEY, R.A., $. М. GLATT& R. $. WILLIAMS, 2004, Allometric length-weight relationships for benthic prey of aquatic wildlife in coastal marine habitats. Wildlife Biology, 10: 241-249.
MEYER, E., 1989, The relationship between body length parameters and dry mass in running water invertebrates. Archiv für Hydrobiologie, 117: 191-203.
MLADENKA, G. C. & G. WAYNE MINSHALL, 2001, Variation in the life history and abundance ofthree populations of bruneau hot springsnails (Pyrgulopsis bruneauensis). Western North American Naturalist, 61: 204-212.
MULLER, O. F., 1774 [1773-1774], Vermium terrestrium et fluviatilium, seu animalium infu-soriorum, helminthicorum et testaceorum, non marinorum, succincta historia, ... Heineck & Faber, Havniae & Lipsiae, 2 vols. [1, [xxx] + 135 pp. (1773); 72 + [viii] pp. (1774); 2, xxxvi + 214 + [x] (1774)].
ROSEMOND, A. D., P. J. MULHOLLAND & J. W. ELWOOD, 1993, Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology, 74: 1264-1280. SADA, D. W., 2008, Synecology of a springsnail (Prosobranchia: Family Hydrobiidae) assem-blage in a western U.S. thermal spring province. The Veliger, 50: 59-71.
SADA, D. W. & G. L. VINEYARD, 2002. Anthropo-genic changes in biogeography of the Great Ba-sin aquatic biota. Pp. 277-293, in: R. HERSHLER, D. В. Madsen & О. В. Currey, eds., Great Basin aquatic systems history. Smithsonian Contribu-tions of the Earth Science, 33: 405 pp. SAMADI, S., J. MAVAREZ, J.-P. POINTIER, В. DELAY & P. JARNE, 1999, Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail Mel-anoides tuberculata: insights into the creation of clonal variability. Molecular Ecology, 8: 1141-1153.
SAVAGE, V. M., J. F. GILLOOLY, J. H.B ROWN, С. В. WEST & E. L. CHARNOV, 2004, Effects of body size and temperature on population growth. The American Naturalist, 163: 429-441.
SILVA, Е. C., J. MOLOZZI & M. CALLISTO, 2010, Size-mass relationships of Melanoides tuber-culatus (Thiaridae: Gastropoda) in a eutrophic reservoir. Zoologia, 27: 691-695.
TAYLOR, D. W., 2003, Introduction to Physidae (Gastropoda: Hygrophila); biogeography, clas-

LENGTH-MASS REGRESSIONS OF FRESHWATER GASTROPODS Пе

sification, morphology. Revista de Biologia Tropical, 51: 1-287.
TRUSSELL, G. C., 2000, Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail. Evolutionary Ecology Research, 2: 803-822.
ОММАСК, Р. J. & W. L. MINCKLEY, 2008, The demise of desert springs. Pp. 11-34, in: L. E. STEVENS & V. J. MERETSKY, eds., Aridland springs in North America. University of Arizona Press, 432 pp.
U.S. ENVIRONMENTAL PROTECTION AGENCY, 1979, Methods for chemical analysis of water and wastes. USEPA, Cincinnati, Ohio, 491 pp. WELCH, А. H., D. J. BRIGHT & L. A. KNOCHEN-MUS, 2008, Water Resources of the Basin and Range Carbonate-rock Aquifer Systems, White

Pine County, Nevada, and Adjacent areas of Nevada and Utah. U.S. Geological Survey Scientific Investigations Report, 2007-5261: 96 pp.
WENZEL, E:, E. MEYER & J. SCHWOERBEL, 1990, Morphology and biomass determination of dominant mayfly larvae (Ephemeroptera) in running waters. Archiv für Hydrobiologie, 118: 31-46.
WOODS, H. A., W. MAKINO, J. B. COTNER, S. E. HOBBIE, J. F. HARRISON, K. ACHARYA & J. J. ELSER, 2003, Temperature and the chemi-cal composition of poikilothermic organisms. Functional Ecology, 17: 237-245.

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